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PREDATION PATTERNS AMONG MOLLUSCS IN THE VICTORIAN TERTIARY

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ABSTRACT: The distinctive boreholes produced by two members of the predatory gastropod families, Muricidae and Naticidae, can be recognised in their molluscan prey in a fossil assemblage from the Victorian Tertiary (Pliocene) from Muddy Creek near Hamilton. Naticids are found to prey mainly on pelecypods with particular concentration on a few genera. Preferential siting of boreholes is established for two species and the degree of shell ornamentation is found to be a deterrent to successful drilling. Muricids are rare but along with naticids show a strong preference for the juveniles of one species of pelecypod.

A review of the literature concerning predation patterns amongst fossil molluscs indicates that the topic has received considerable attention. Almost certainly, this is due to the fact that it is one of the few areas where a mathematical approach can be applied to palaeopredation (Reyment 1971). Predatory gastropods that attack by drilling holes into the shells of their prey can be divided into two groups. The family Naticidae (order: Mesogastropoda) and the family Muricidae (order: Neogastropoda) are the main predatory gastropods and they show distinct differences in borehole morphology allowing each hole to be classified as to the family of the predator. The method by which the holes are drilled with the radula by these gastropods has been studied by a number of workers (Jensen 1951, Carricker 1961, Carricker and Yochelson 1968, Vermeij 1980) and the result is strong confirmation for an unequivocal determination of the type of gastropod based on the bore shape. Naticids drill a parabolic hole with a countersunk margin whereas muricids drill a more cylindrical steep-sided bore with no countersinking. A schematic diagram of both types of drill is shown in Fig. 1.

The site from which the fossils were collected is Macdonald Bank on the Muddy Creek, 6 km west of Hamilton, Victoria. A section of the bank was cleaned of weathered surface and a cubic sample (volume 27 dm³) was collected and analysed. The age of the assemblage is Lower Pliocene (Douglas and Ferguson, 1976) and it is usually referred to as the Grange Burn Coquina. Identification of the species present in the sample was carried out by Dr. T. A. Darragh of the Museum of Victoria.

RESULTS AND DISCUSSION

The species collected and number of specimens drilled or partially drilled are shown in Tables 1 and 2. Table 3 shows the species ranked in order of predation intensities. Only those species with ten or more individuals in the sample were placed in the ranked table. *Placamen subroboratum*, *Glycymeris halli* and *Sunetta gibberula* are the preferred species for naticids amongst the pelecypods, whilst muricids select *Notocorbula ephamilla*. Amongst the gastropods, naticids and muricids both prefer *Niotha crassigranosa* with other species showing little predation. There is some evidence of cannibalism with *Polinices cunninghamensis*—the dominant predatory gastropod sampled—showing a 1% attack rate. Reporting on cannibalism amongst gastropods from Ameki, Nigeria, Adegoke and Tevesz (1974) found naticid/naticid predation levels of 15%. Carricker (1961) reported cannibalism in laboratory starved specimens of naticids; and noted that when bivalve prey was presented, the naticids abandoned cannibalism. The greatest proportion (>99%) of naticids are *Polinices cunninghamensis* and presumably this species is responsible for most of the naticid boreholes observed.

Although no muricids were found in the study sample, they have been recorded from the Muddy Creek locality. In a catalogue of Tertiary Mollusca from Australia, Darragh (1970) lists ten muricid genera, including two species of *Bedeva*, whose type locality is the Muddy Creek deposits.

Naticids accounted for between 70% and 75% of all successful drills in gastropods and pelecypods whilst muricids accounted for 25% of gastropod and 15% pelecypod drillings.

The number of left and right valves was counted for *Sunetta gibberula*, *Notocorbula ephamilla* and *Ennucula kalimnae*, and the total number of left hand valves was not significantly different from the total number of right hand valves. For individual species, there appears to have been some *post mortem* sorting; but overall the assemblage, as represented by these three species, would seem to have come from shallow water close to the shoreline.

Distribution of drilled holes in pelecypod shells

The two species chosen for this investigation were *Sunetta gibberula* and *Glycymeris halli*. This choice was made in view of the need to have adequate sample numbers for the statistical analysis. The data for the analysis were obtained by projecting an image of the valve onto a screen using an overhead projector. The projector was moved until the shadow of the valve coincided with the outline traced from a typical valve of median size. By using this method, the position of the borehole showed as a spot of light and it was possible to obtain relative positions of boreholes regardless of the size of the valve. Figure 2 shows the scatter diagram for

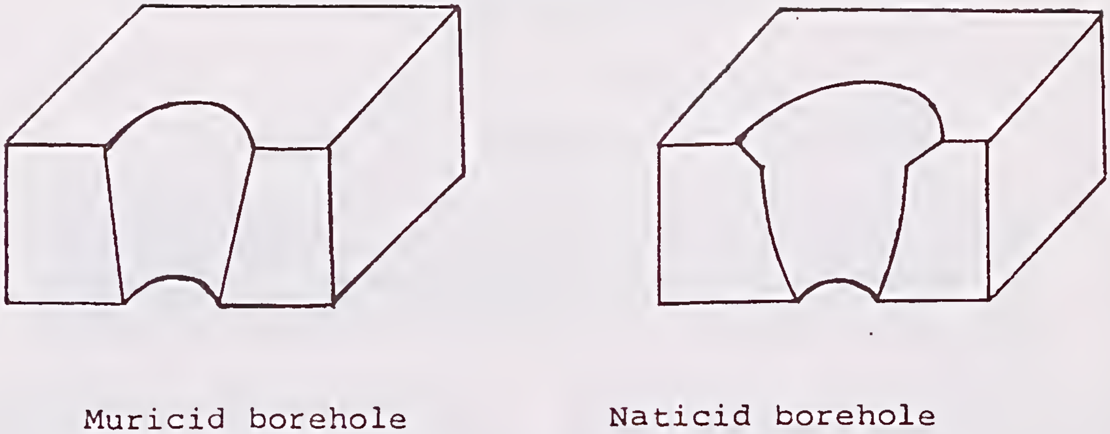

Fig. 1—Typical predation boreholes by muricids (left) and naticids (right).

TABLE 1
OCCURRENCE OF DRILLHOLES IN GASTROPODS FROM THE GRANGE BURN COQUINA

Species	Total Examined	Drilled Naticid	Drilled Muricid	Failed Drills
Allocospira papillata (Tate)	50	1		1
Austromitra sp.	1	1		
Gemmaterebra catenifera (Tate)	25	2		
Polinices cunninghamensis (Harris)	205	3		
Semicassis wannonensis (Tate)	1	1		
Sydaphera wannonensis (Tate)	8	1		
Niotha crassigranosa (Tate)	72	5	5	

No evidence of drilling was found in *Amaca triplicata* (Tate), *Amblychilepas* sp., *Amorena masoni* (Tate), *Ancilla* sp., *Cominella* sp., *Cymatiella verrucosa* (Reeve), *Euriclanculus eucarinatus* (Ludbrook), *Leiopyrga quadricingulata* (Tate), *Marginella* sp., *Polinices subinfundibulum* (Tate), *Polinices subvarians* (Tate).

G. halli with the arbitrary quadrats chosen for the analysis. The method of statistically treating the data obtained follows that of Reyment (1971, p. 140) in that the data were compared with a theoretical Poisson distribution and tested for goodness of fit with a chi squared test. The calculations are set out in the Appendices. The chi squared calculation was performed on the pooled data of several cells to avoid the problem of any expected cell frequency being less than 5. Kreyszig (1970, p. 249) mentioned that failure to pool classes in such cases may give unreliable results. The results of the analysis showed that the observed distribution differed significantly ($p<0.05$) from a Poisson distribution and that the siting of attack is not random for naticid predation of *G. halli*. The preferred area is readily seen on the scatter diagram and lies in the median section of the valve commencing at a quarter of a diameter from the umbo and extending to three-quarters of a diameter from the umbo. No preference for either side of the valve was found, with 27 borings to the left side of the arbitrary bisector and 29 borings to the right. This could be expected in a pelecypod like *G. halli* which has a perfectly symmetrical shell and there would be no orientation clues to enable a predator to drill either side selectively. In view of the symmetrical nature of the shell and

TABLE 2
OCCURRENCE OF DRILLHOLES IN PELECYPODS FROM THE GRANGE BURN COQUINA

Species	Total Examined	Drilled Naticid	Drilled Muricid	Failed Drills
Ennucula kalimnae (Singleton)	158	9		1
Gari hamiltonensis (Tate)	9	2		
Glycymeris sp.	16	1		
Glycymeris halli (Prichard)	309	56	10	2
Limopsis beaumarisensis (Chapman)	26	1		
Notocorbula ephamilla (Tate)	184	15	8	5
Ostrea sp.	4	Indeterminate drills		
Placamen subroboratum (Tate)	103	15	2	9
Sunetta gibberula (Tate)	187	28	3	1
Tawera propinqua (Tenison Woods)	21		1	

No evidence of drilling was found in *Chlamys antiaustralis* (Tate), *Keria johnstoni* (Tate), *Limopsis depressa* (Chapman), *Myadora corrugata* (Tate), *Neotrigonia strangei* (McCoy), *Pleuromeris pecten*, *Scaeoleda* sp., *Tucetona convexa* (Tate).

the preferred sitings of the boreholes, it is possible that predatory naticids used the pronounced umbo of this bivalve to orient themselves to a central position on the valve.

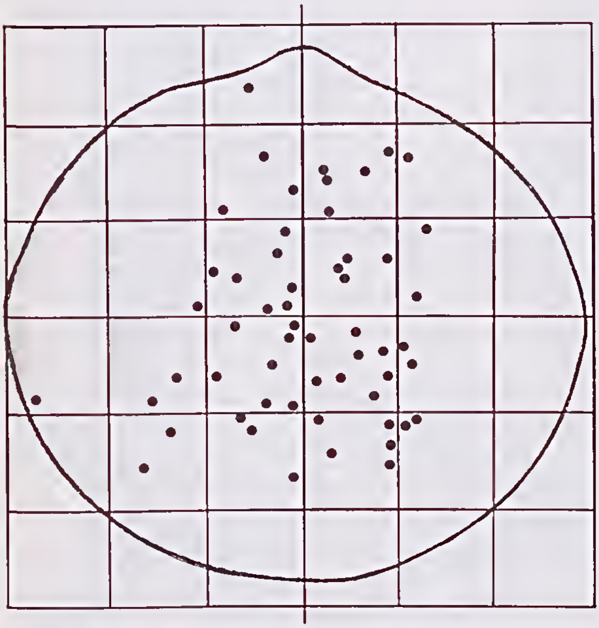

Fig. 2—Scatter diagram for naticid predation on *Glycymeris halli*.

Sunetta gibberula was examined in a similar manner to *G. halli* using an overhead projector to compensate for size differences. This pelecypod has an asymmetric valve and separate scatter diagrams are given for right and left valves (Figs. 3, 4). When the valves were examined it was found that there was a statistically significant preference in the right valve for the side furthest from the umbo. The left valves showed the same tendency with raw data but it was not statistically significant. In view of this, the data from both valves were pooled on a scatter diagram (Fig. 5) and a chi squared test applied to these data. The results show that naticids prefer to drill the side furthest from the umbo ($p<0.05$). A comparison of observed frequencies of boreholes in the arbitrary quadrats versus a Poisson distribution was also carried out for *S. gibberula* and the result demonstrates that naticids have a preferential site of attack on this bivalve more pronounced than the site preference in *G. halli*. Thus it appears that the asymmetric nature of the valves in this case provides predators with an additional orientation clue above that of the umbo, and that in the case of *S. gibberula* there is a significant tendency to be drilled in the central region of the shell favouring the side furthest from the umbo. Edge drilling was found in only 2% of *G. halli* and *S. gibberula*. On the other hand, Vermeij (1980) found edge drilling to be a significant site of attack by naticids and muricids on recent bivalves in Guam. However, the comparisons between Victorian Tertiary and Recent Pacific deposits is too large a spatial and temporal gulf to expect any correlation.

Because only three muricid bores were found on *S. gibberula* it was not possible to make any statistically meaningful comment upon their distribution; however in all three cases the site of attack was on the side adjacent to the umbo (sites marked "M" in Fig. 5).

The other two species with significant predation percentages, viz. *Placamen subroboratum* and *Notocorbula ephamilla*, did not have sufficient drilled valves to allow any significant results to come from fitting their predation pattern to a Poisson function.

Gastropod predation

Amongst the gastropods, only *Niotha crassigranosa* showed evidence of being a major prey species of other predatory gastropods. The degree of muricid drilling

TABLE 3
PREDATION INTENSITIES ON GASTROPODS AND PELECYPODS IN THE GRANGE BURN COQUINA

Species	% drilled	% naticid	% muricid	% failed
Pelecypoda				
Placamen subroboratum	25	57	7	36
Glycymeris halli	22	82	15	3
Sunetta gibberula	17	88	10	2
Notocorbula ephamilla	15	54	28	18
Ennucula kalimnae	6	90	0	10
Glycymeris sp.	6	100	0	0
Limopsis beaumarisensis	4	100	0	0
Total pelecypod predation intensity (all collected species)	16	75	15	10
Gastropoda				
Niotha crassigranosa	14	50	50	0
Gemmaterebra catenifera	4	100	0	0
Allocospira papillata	2	50	0	50
Polinices cunninghamensis	1	100	0	0
Total gastropod predation intensity (all collected species)	5	70	25	5

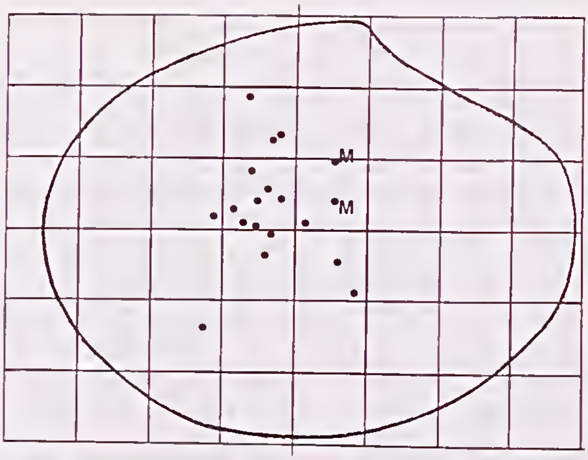

Fig. 3—Naticid predation pattern on right valve of *Sunetta gibberula*.

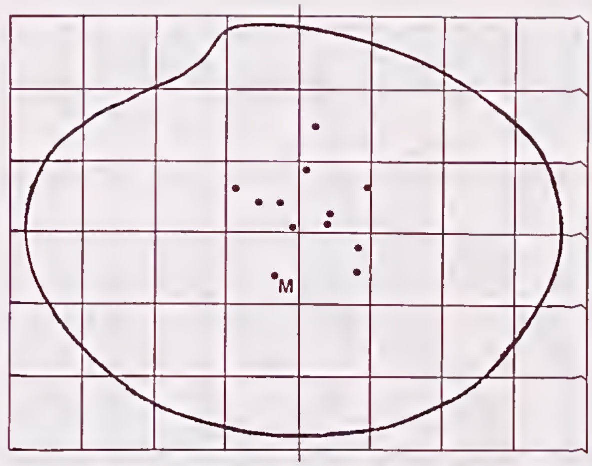

Fig. 4—Naticid predation pattern on left valve of *Sunetta gibberula*.

was high in this species. For both naticids and muricids, in 8 out of 10 cases of drilling, the site was on the penultimate whorl. Adegoke (1974) finds that in the Eocene of Nigeria no preferences can be established for gastropod/gastropod predation despite the fact that gastropods were the favoured predator food source.

Shell texture and drilling frequency

There are conflicting reports in the literature regarding the effect of ornamentation on drilling frequencies in pelecypods. Some authors have pointed to strong external sculpture as a trait that should prevent drilling (Reyment 1967, Taylor 1970). Other authors have found either no relationship (Vermeij 1980, Adegoke and Tevesz 1974), or one that suggests strongly sculptured valves have higher drilling frequencies than do smoother valves (Robba and Ostinelli 1975). Table 4 shows the results from this study. It appears that strong ornamentation is associated with drilling failures. *Placamen subroboratum*, in particular, is a preferred species for naticid attack yet also shows the highest failure rate. Some method of quantifying the degree of ornamentation (Figs. 6, 7) is needed before any statistical analysis can be done on the relationship between drilling and ornamentation.

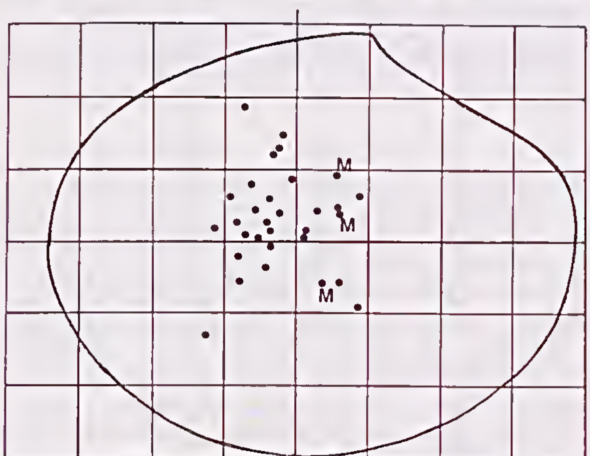

Fig. 5—Combined scatter diagram for *Sunetta gibberula*. Note that muricid bores are marked "M".

TABLE 4
SHELL ORNAMENT AND DRILLING FREQUENCIES

Species	Ornamentation	% Unsuccessful Drills
Placamen subroboratum	Strong lamellae	8.7
Notocorbula ephamilla	Moderate lamellae	2.7
Glycymeris halli	Weak radial ribs—smooth	0.6
Sunetta gibberula	Smooth	0.5

Preference for small prey

A number of investigators (Reyment 1966, Taylor 1970, Adegoke and Tevesz 1974) have concluded that naticids and muricids have a tendency to prey upon the smaller members of a population. Investigation of this concept involves comparing the mean and standard deviation of the drilled sample with the mean and standard deviation of the undrilled population and assessing for significant difference by a Student's t test (Table 5). The full calculations for *G. halli* are set out in Appendix 3, including an example of a modified method recommended by Freund (1973, p. 227) when dealing with small samples. In all cases, except *G. halli*, muricid and naticid drilled specimens were pooled to increase sample size. Significant preference was found for smaller bivalves only in *G. halli*; both muricid and naticid predators showing a preference for the juveniles of this species (Table 6). In the other cases, the drilled samples could reasonably be expected from the population by chance, often enough to make the differences of no significance.

CONCLUSIONS

The major predator found in this study was the naticid, *Polinices cunninghamensis*. This gastropod preys preferentially on bivalves, particularly *Placamen*

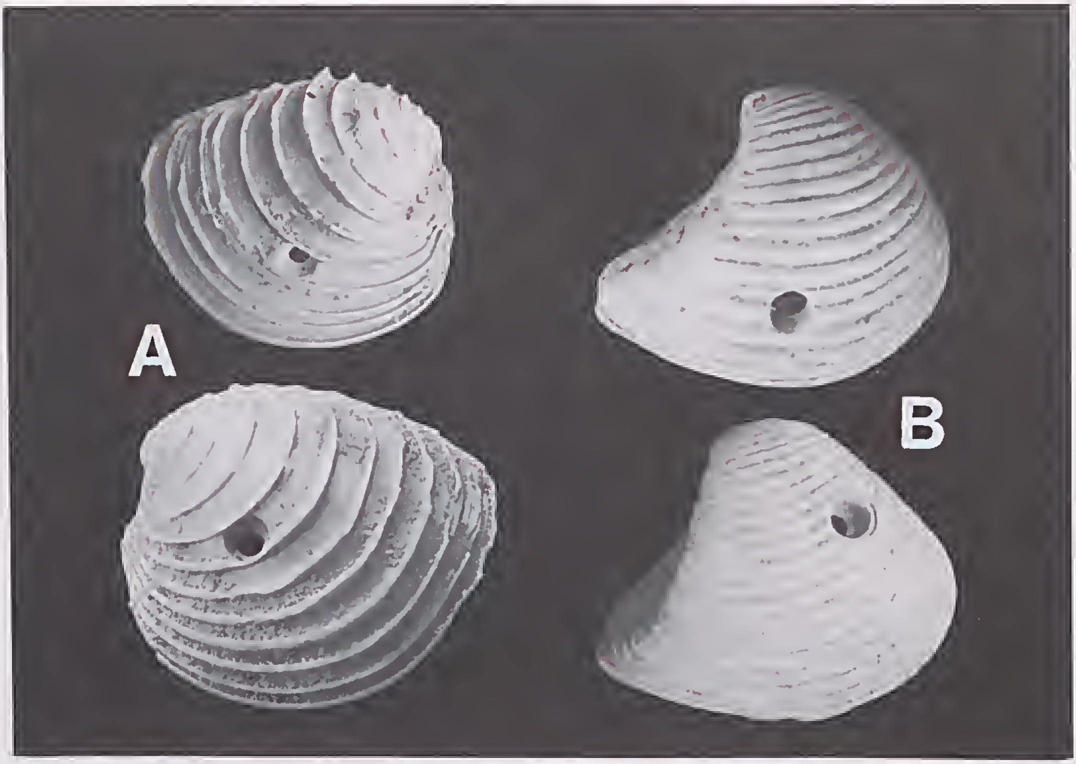

Fig. 6—Gastropod predation in the Grange Burn Coquina. A, *Placamen subroboratum*: Evidence of predation. The valve on the top has one successful and one failed drilling attempt. Note the degree of ornamentation. B, *Notocorbula ephamilla*: above—muricid borehole; below—naticid borehole.

subroboratum, *Sunetta gibberula* and *Glycymeris halli*. The morphology of the holes drilled by this naticid is the typical countersunk paraboloid and is readily distinguished from muricid boreholes. Naticids and muricids were found to prey preferentially on juveniles of the species, *G. halli*, but preferences for juveniles of other species could not be established with confidence. The distribution of boreholes on *G. halli* was not random and the predator possibly used the pronounced umbo of this symmetrical pelecypod to orient itself whilst drilling. No preference was found for either side of the valve but there was a significant preference for the central area.

The asymmetrical bivalve, *S. gibberula*, was also found to have a preferred area of attack. In this case, there was an even stronger preference for a central region on the opposite side to the umbo. It is possible that the pronounced asymmetrical umbo gives naticids a more specific orientation clue than is the case with *G. halli*.

Shell texture was found to be a significant impediment to successful drilling. The heavily ornamented

TABLE 5
MEAN AND STANDARD DEVIATION OF MAXIMUM DIMENSIONS IN CM OF DRILLED AND UNDRILLED PELECYPODS

Species	Undrilled population			Drilled sample			t value
	n	$\bar{x}$	x	n	$\bar{x}$	s	
Glycymeris halli (naticid drilled)	240	1.55	0.36	56	1.38	0.30	3.69
Glycymeris halli (muricid drilled)	240	1.55	0.36	9	1.37	0.21	2.42
Sunetta gibberula	156	2.05	0.30	32	1.98	0.31	1.23
Placamen subroboratum	78	1.85	0.32	26	1.80	0.33	0.65
Ennucula kalimnae	133	1.67	0.16	10	1.64	0.19	0.46

N = sample size $\bar{x}$ = mean s = standard deviation

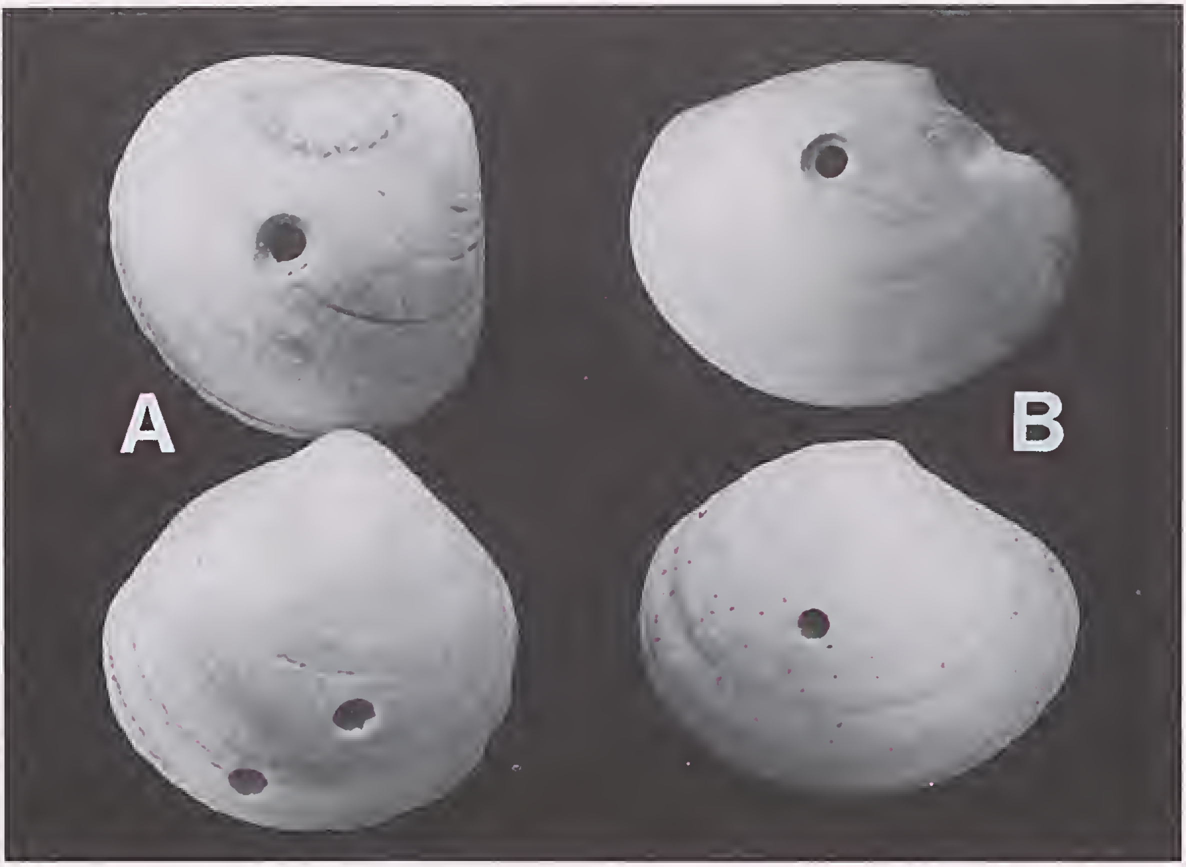

Fig. 7—A, *Glycymeris halli*: above—naticid borehole; below—two successful muricid boreholes on the one valve. B, *Sunetta gibberula*: above—naticid borehole; below—muricid borehole.

pelecypod, *P. subroboratum*, whilst being a preferred prey species, showed a high level of unsuccessful drilling attempts; whilst *S. gibberula*, a smooth pelecypod, pro vided evidence of very few unsuccessful attacks. Othe bivalves of intermediate ornamentation showed corresponding intermediate failure rates.

The main contentious issues in these conclusions are the evidence for ornamentation being a drilling deterrent and that the drills are clustered in particular patterns. The summary presented in Table 7 shows the basic findings from this study compared with those of other workers using similar materials and methods. The data suggesting preference for small prey are only at variance with the work of Vermeij (1980), and this preference could be more firmly established with a study designed wholly to test the hypothesis with samples large enough to return unequivocal findings. A similar larger sample size would clarify the situation regarding the preferred site of attack. Underpinning all of these attempts at a reconciliation of varying conclusions is the possibility that, given the time and space differences between different studies and their varied faunas, a pattern of

TABLE 6
SIGNIFICANCE OF t TESTS ON DRILLED AND UNDRILLED PELECYPODS

Species	t value	Frequency of t value being obtained by chance	Conclusion
Glycymeris halli (naticid drilled)	3.69	0.001	Significant preference for smaller pelecypods.
Glycymeris halli (muricid drilled)	2.42	0.03	Significant preferences for smaller pelecypods.
Sunetta gibberula	1.23	0.2	No significant preference.
Placamen subroboratum	0.65	0.5	No significant preference.
Ennucula kalimnae	0.46	0.7	No significant preference.

TABLE 7
COMPARATIVE CONCLUSIONS FROM SEVERAL CAINOZOIC MOLLUSCAN PALAEOPREDATION STUDIES

Feature	Recent Guam Reef Flats (Vermeij 1980)	Recent Nigerian Shelf (Reyment 1966)	European Eocene (Taylor 1970)	Nigerian Eocene (Adegoke and Eocene 1974)	Victorian Miocene (this study)
Principal predatory bores	muricids	naticids	naticids	naticids	naticids
Incidence of cannibalism amongst naticids	—	high	high	high	low
Favoured predator food source	bivalves	bivalves	gastropods	gastropods	bivalves
Muricid abundance in assemblage	abundant	abundant	few	rare	rare
Borings concentrated on particular parts of valve in bivalve	—	yes	yes, in naticid borings on gastropods	no	yes
Shell sculpture as a deterrent to boring	no	—	yes	no	yes
Preference for small prey	no	yes	yes	yes	yes, in *G. halli*

palaeopredation might emerge in each epoch and area which is unique to that time and location. Thus, there may not be a general conclusion to be drawn about preferred sites of attack by naticids on pelecypods but only conclusions which are relevant for a particular fossil assemblage.

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APPENDIX 1

OBSERVED AND THEORETICAL FREQUENCIES FOR NATICID PREDATION ON *Glycymeris halli*.

Number of holes per square (x)	Observed frequencies (f)	Poisson probability	Theoretical frequencies
0	7	0.101	2.43
1	4	0.232	5.57
2	5	0.266	6.37
3	2	0.203	4.86
4	1	0.116	2.78
5	2	0.053	1.28
6	1	0.020	0.49
7	1	0.007	0.16
8	1	0.002	0.05
	24		23.99

Mean = 2.29 holes per square; variance = 5.69; standard deviation = 2.38; coefficient of variation from a Poisson distribution = 1.04.

CALCULATION OF χ^2 FOR A GOODNESS OF FIT OF NATICID PREDATION ON *G. halli* TO A POISSON DISTRIBUTION.

Number of holes per square	Observed distribution O	Expected distribution E	$\chi^2 = \frac{(O-E)^2}{E}$
0-1	11	8	1.12
2	5	6.37	0.29
3-4	3	7.64	2.81
5 and more	5	1.98	4.61
			$\chi^2 = 8.8$

APPENDIX 2

OBSERVED AND THEORETICAL FREQUENCIES FOR NATICID PREDATION ON *Sunetta gibberula.*

Number of holes per square (x)	Observed frequencies (f)	Poisson probability	Theoretical frequencies
0	23	0.393	11.80
1	2	0.367	11.01
2	1	0.171	5.14
3	0	0.053	1.60
4	2	0.012	0.37
5	1	0.002	0.07
6	0	0.0003	0.01
7	0	0	0
8	0	0	0
9	0	0	0
10	1	0	0
	30		30.0

Mean = 0.93 holes per square; variance = 5.56; standard deviation = 2.36; coefficient of variation from a Poisson distribution = 2.53.

CALCULATION OF χ^2 FOR A GOODNESS OF FIT OF NATICID PREDATION ON *S. gibberula* TO A POISSON DISTRIBUTION.

Number of holes per square	Observed distribution O	Expected distribution E	$\chi^2 = \frac{(O-E)^2}{E}$
0	23	11.80	14.87
1	2	11.07	7.37
2	1	5.14	3.33
3 and more	4	2.05	1.85
			$\chi^2 = 27.42$

APPENDIX 3

STUDENT'S t TEST CALCULATION ON *Glycymeris halli.*

Population	Naticid drilled	Muricid drilled
Number (N) Np = 240	$N_n = 56$	$N_m = 9$
Mean $\bar{x}$ $\bar{x}_p = 1.55$	$\bar{x}_n = 1.38$	$\bar{x}_m = 1.37$
Standard deviation s $s_p = 0.36$	$S_n = 0.30$	$S_m = 0.21$

t = 3.69 with 239 degrees of freedom.
Modified method for smaller samples (Pollard 1968, p. 102).
Example for muricid bored *G. halli* sample.

$$t = \frac{\bar{x}_p - \bar{x}_m}{S_m} \times \sqrt{N-1}$$

$$= \frac{1.55 - 1.37}{0.21} \times \sqrt{9-1} = 2.42$$

t = 2.42 with 8 degrees of freedom.